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ON THE SENSITIVITY TO LOW pH OF SOME SELECTED FRESHWATER CRUSTACEANS (DAPHNIA AND GAMMARUS, CRUSTACEA)

J. BREHM and M.P.D. MEIJERING

With 6 Figures in the text

Abstract

In natural habitats *Daphnia magna* and *Daphnia pulex* have different ranges of extension with respect to pH-conditions in ponds. In acid brooks *Gammarus pulex* will survive longer than *Gammarus fossarum*. Investigations in the laboratory showed that, correspondingly, *D. magna* is more sensitive to low pH than *D. pulex*, and *G. fossarum* more sensitive than *G. pulex*. Mortality increased in close relation to increasing acidity and is mainly caused by the increasing concentration of free hydrogen ions. Anions are less important, which was shown in experiments with five different acids, including acid drip water from a fir forest. Low pH-values may lead to the mobilization of heavy metal ions, which can increase the toxicity of a medium. Under experimental conditions crustaceans can improve pH-values when they release ammonia and amino-acids. The limnological importance of this behaviour is briefly discussed.

Introduction and problem

Measuring pH levels has long been a standard test in limnology, but in contrast to oxygen concentrations, salinities, or temperatures, for instance, pH levels are rarely discussed in detail, for example in their capacity as limiting ecophysiological factor which has a decisive influence on the distribution of aquatic organisms. Only in recent years have studies on the physiological effect of low pH levels on Cladocera been published - on survival and reproduction (DAVIS & OZBURN 1969), respiration (IVANOVA & KLEKOWSKI 1972; ALIBONE & FAIR 1981), osmoregulation (POTTS & FRYER 1979), and filtration rates (IVANOVA 1969; KRING & O'BRIEN 1976). These studies involved both long-term adaptation experiments within a relatively narrow pH range around the neutral point and very short-term stress tests at extreme pH levels. COSTA (1967) specifically investigated the locomotor activity of Gammarus pulex in highly acidic medium.

In freshwater crustaceans, pH levels obviously have limiting effects on distribution. This becomes clear for example from the field tests by ÖKLAND (1969) with Gammarus lacustris in Norwegian lakes and from experiments by BÖRGSTRÖM & HENDREY (1976), according to which almost all G. lacustris die in the course of 45 h at pH 5.5. Field tests by TEICHMANN & MEIJERING (1981) on Gammarus pulex and Gammarus fossarum in flowing waters in Hesse and by MEIJERING (1970) on Daphnia magna and Daphnia pulex in ponds on the East Friesian island of Spikeroog resulted in similar findings. Decreasing pH levels first cause acid-sensitive species to disappear. The acidification in the field tests may be anthropogenic (BREHM 1980).

According to the distribution pattern in terms of time and locality in water bodies, Gammarus pulex should be less sensitive

to acid than its sister species G. fossarum. Of the species pair Daphnia magna and D. pulex, the latter should be more acid-resistant. To elucidate this matter, laboratory tests, in addition to the field tests, were carried out on the obviously different acid sensitivities of these four crustacean species.

Material and methods

The test individuals were reared from the mud of ponds on the East Friesian island of Spikeroog - Daphnia pulex LEYDIG from pond f in the dunes and Daphnia magna STRAUS from pond p in pastures that occasionally are flooded by the sea. For the limnological details of these temporary small water bodies see MEIJERING (1970) and JACOBI & MEIJERING (1979). D. pulex was reared in water from pond f, D. magna in an infusion of cattle dung. The temperatures for both rearing and tests were 20-22°C (summer temperatures in the ponds).

The gammarids required for the experiments were caught in the lower part of the Rimbach in the "Schlitzerland"*, Eastern Hesse, where Gammarus pulex L. and Gammarus fossarum KOCH occur with equal abundance (MEIJERING 1971). In the laboratory they were kept in water from the Rimbach or in "Schlitz" water (from the test raceways of the Limnological River Station, KOCH-KALLNBACH & MEIJERING 1977) at temperatures of 10-15°C (summer temperatures in forest brooks); the tests were carried out at the same temperatures.

In the test on specific acid sensitivity of the four selected crustacean species, pH levels in the range of 7.0 - 3.0 were investigated. To produce the desired pH, the more or less neutral test water from pond f, the dung infusion, the Rimbach or the Schlitz water was acidified with sulphuric acid, hydrochloric acid, phosphoric acid, citric acid, or the drip water from a spruce

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* Translator's note: Region around the town of Schlitz

forest in the Schlitz region that was also relatively acidic. The spruce drip water contained a complex mixture of organic acids (resin, tannic, fulvic and humic acids) that are washed from trees and ground litter by precipitation and not infrequently cause the sudden death of fish in brooks or cause various animal and plant species to disappear permanently (BREHM 1980). Such drip water frequently also contains free sulphuric acid from precipitation (partly anthropogenic air pollutants).

In order to determine the specific effect of hydrogen ions (independently of overlying effects of the specific acid residues or non-dissociated acid molecules) on the selected crustaceans, parallel tests with the various acids were required. Usually the conductivity of the test media was around 200 μS_{20}/cm; only in the Daphnia tests with dung infusion it was increased to approx. 400 μS_{20}/cm. All test results are, however, comparable with each other (same order of magnitude of osmotic values and hypotonicity of all test media).

In the Daphnia tests, 8-10 amictic adult females each were kept in vessels with 50 mL water. They were monitored at intervals of about 2 h (counting survivors). In the gammarid tests, 8-10 adult males each were held in vessels with 200 mL water, and they, too, were monitored at 2-h intervals (counting survivors, counting obviously injured, more or less immobilized individuals, observing discharge and re-ingestion of excrements).

The tests lasted for a minimum of 24 h each (in continuous light), but the results were evaluated after each 12-h exposure since after longer periods the pH of the test medium frequently rose considerably (Figures 1 and 4). The crustaceans were placed in the water at the earliest 4-6 h after acidification since during that time the pH could rise notably even without crustaceans (delayed neutralization of added acids; gradual volatilization of

carbon dioxide, thus lowering the concentration of the carbonic acid released from hydrogen carbonate by acidification). The experimental pH level appropriately is the mean pH level of the first 12 h of test, since even then (small) pH gradients have to be expected.

The following measuring instruments were used: Precision pH meter (type 350, Knick) for test water pH, laboratory conductometer (type LBR, Wissenschaftlich-Technische Werkstätten) for conductivity, and a fully automatic analyzer (Autoanalyzer, Technicon) for ammonium concentrations which occasionally were measured.

Results

1. Field experiments

On the island of Spikeroog, Daphnia pulex had hitherto been observed at pH levels of 7.5 - 4.5 (MEIJERING 1970, JACOBI 1977), Daphnia magna at pH 10.0 - 6.0 (according to the same authors). Gammarus pulex and Gammarus fossarum had also been reported as occurring in the Schlitzerland, eastern Hesse (MEIJERING 1971), but without any reference to the pH levels of the investigated bodies of water. When gammarid distribution was now compared with the brook pH levels also measured at that time (data for late winter 1967/68; 75 measuring points) the following was established (Figure 2): Below pH 6, G. pulex was found rarely, G. fossarum only very rarely. At pH below 5, both gammarids were absent altogether. Specifically, G. pulex was observed at pH 7.6 - 5.1, G. fossarum at pH 8.2 - 5.4.

2. Laboratory experiments

Figure 3 shows the survival curves of Daphnia pulex in media which, parallel to three different acids, had been adjusted

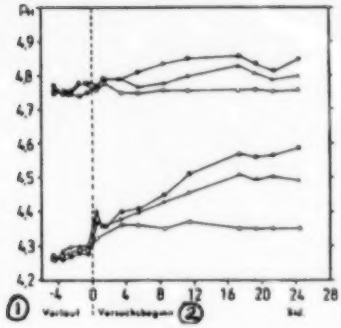

Figure 1. pH values in brook water (Rimbach) after acidification (with spruce drip water) with and without gammarids. White symbols - without gammarids; solid symbols - with gammarids (● = Gammarus pulex; ▲ = G. fossarum)

Translator's note: In Figures, where applicable, please read commas as decimal points.

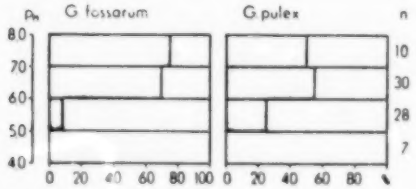

Figure 2. Occurrence of two Gammarus species in forest and meadow brooks of the Schlitzerland as a function of pH level (data from late winter).
n = number of sampling points

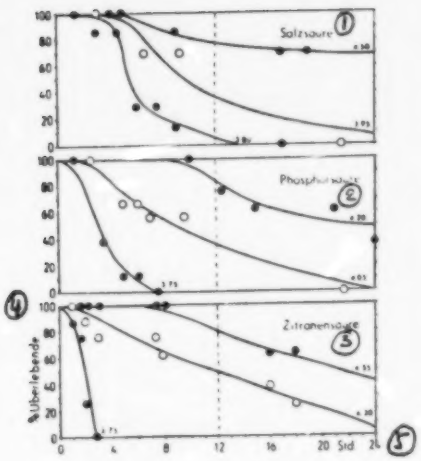

Figure 3. Survival curves (hand-drawn) of Daphnia pulex as a function of pH level and added acid. Mean pH levels next to each curve.

1 - hydrochloric acid
2 - phosphoric acid
3 - citric acid
4 - % survivors
5 - hours

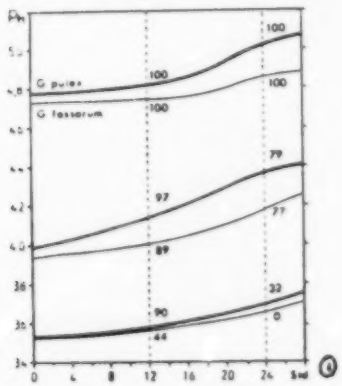

Figure 4. pH levels (hand-drawn curves) in a selected test on the acid sensitivity of two Gammarus species. Figures give the percentage of surviving individuals after 12-h and 24-h exposure in acidified medium

1 - hours

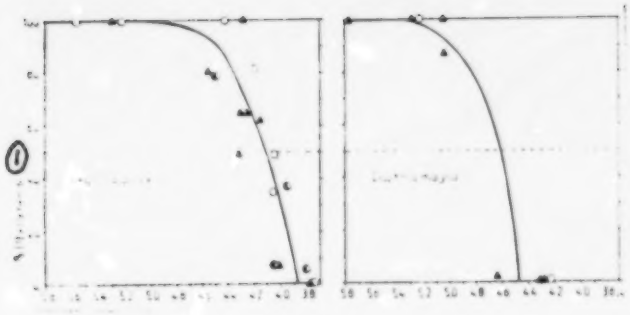

Figure 5. Acid sensitivity (in % survivors after 12-h exposure in acidified pond or dung water; hand-drawn curves) of two Daphnia species.
Acidification: ▲ with citric acid, o with phosphoric acid, ● with hydrochloric acid.

1 - % survivors

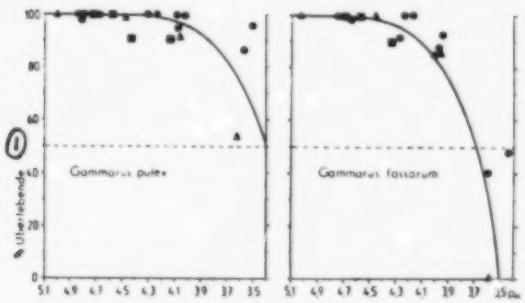

Figure 6. Acid sensitivity (in % survivors after 12-h exposure in acidified brook water; hand-drawn curves) of two Gammarus species.
Acidification: ▲ with citric acid, ■ with sulphuric acid, ● with spruce drip water.

1 - % survivors

to three different low pH levels. In all three test series, mortality distinctly increased with decreasing pH. Of the acids tested, citric acid had the strongest effect, hydrochloric acid the weakest; phosphoric acid ranged in between.

Figures 1 and 4 show that during the experiments, pH levels drifted to a greater or lesser extent, showing a rising tendency, especially in the experiments with Gammarus pulex and at test periods exceeding 12 h (disregarding a certain lead time during which pH levels tended to rise even in the absence of the test individuals; Figure 1).

Figure 5 depicts the survival rates of Daphnia pulex and D. magna (12-h exposure) as a function of experimental pH levels. The critical pH range for D. magna was 5.3 - 4.5. D. pulex, with a critical pH range of 4.9 - 3.9, proved much more acid resistant. The type of acid used had only little effect (see also Figure 3).

Figure 6 shows the acid sensitivity of the two tested Gammarus species. Under the prevailing conditions, the critical pH levels for G. pulex started from 4.3 downward, for G. fossarum already at approx. 4.6. The spruce drip water used for acidification was less toxic than the individual acids added (citric acid, sulphuric acid).

Discussion

Acidification of the medium by means of various acids - hydrochloric acid, sulphuric acid, phosphoric acid, citric acid, spruce drip water - had the same basic harmful effect on Daphnia and Gammarus. Hydrogen ion concentration in the medium can therefore be regarded as the decisive factor, with acid residues playing only a subordinate role, at least for the acids tested here. The situation would be different for carbonic acid, which we deliberately did not use: It is a product of respiration that even at

relatively low concentrations inhibits breathing or has toxic effects. Moreover, no low pH levels could be adjusted using carbonic acid since, being a weak acid, it does not dissociate sufficiently.

Various physiological effects of increased hydrogen ion levels have already been described. Obviously, respiration is the primary victim. At a slight decrease of pH levels, the respiratory rate, like the filtration rate, first rises, as IVANOVA & KLEKOWSKI (1972) observed in the waterflea Simocephalus vetulus. This reflects emergency breathing which, upon further extreme decreases of pH levels, finally breaks down. ALIBONE & FAIR (1981), in Daphnia magna, showed this to be caused by difficulties in the carbon dioxide exchange with the medium. Furthermore, in Daphnia magna, osmoregulation is impaired at pH levels below 5, as POTTS & FRYER (1979) demonstrated from the sodium uptake rates. At lower pH levels the crustaceans also become more mobile. COSTA (1967), for instance, by decreasing pH levels below 6.2, triggered flight reactions in Gammarus pulex, which typically were more pronounced for acidification with carbonic acid than with hydrochloric acid.

To these short-term effects of extreme pH decreases are added long-term effects of slight deviations from optimum pH levels, as reflected for instance in the reproduction rates. According to DAVIS & OZBURN (1969) and to SCHEITHAUER & BICK (1964) the optimum pH for Daphnia pulex is 7 - 8.5.

In our own (short-term) experiments, pH levels in the medium (apart from physical and chemical causes of pH changes) rose due to defecation and excretions. The increase in pH levels was especially noticeable for Gammarus pulex (large individuals!), at test periods exceeding 12 h, and at low pH buffering capacity of the medium (acidification with strong inorganic acids such as hydrochloric and sulphuric acids). According to GARDNER & SCAVIA

(1981) crustaceans, among them Daphnia pulex and D. magna, excrete ammonia as an end product of nitrogen metabolism. Moreover, amino acids pass into the medium in excretions and excrements, as BREHM (1967) proved experimentally specifically for Daphnia magna. In a separate experiment it was confirmed that the situation was the same for Gammarus pulex. After a test period of 24 h, the ammonium and amino acid concentrations had risen from the initial levels of 0.12 mg N/L to only 0.18 mg N/L in the blank test, but to a mean of 0.51 mg N/L in the vessels with gammarids.

Ammonia and amino acids (to the extent they have not already formed dipolar ions with NH_3^+ groups) bind H^+ ions ($NH_3 + H^+ \rightarrow NH_4^+$ or $AS\text{-}NH_2 + H^+ \rightarrow AS\text{-}NH_3^+$; AS = amino acid, $-NH_2$ = free amino group), thus raising pH levels in the medium. Living conditions accordingly improve for individuals in the previously acidified water, so that, provided test periods are prolonged and initial pH levels not too low, they can recover even during the experiment. This could be easily verified from mobility and, in the case of the gammarids, from discharge and re-ingestion of excrements. Gammarids, for example, discharged abundant excrements in not overly acidic medium, to be re-ingested later. At very low pH levels, serious injury or death occurred to soon that hardly any excrements were discharged. Where this did happen, they were not re-ingested. In some experiments in moderately acidic medium, gammarids (Figure 1) reacted by shock reflected in an abrupt rise in pH levels at the beginning of the experiment (sudden, increased excretion?). Perhaps this pH increase was caused partly or wholly by dissolution of the calcium compounds in the carapace.

In the field, animal-related increases in pH levels may have great ecophysiological importance if as a result the habitats of the Daphnia (e.g. dune ponds tending to acidification, in some

of which these small crustaceans occur in great abundance) or of the gammarids (e.g. the bottom of temporarily acidic brooks in the region of swamps or extensive spruce forests) threaten to become temporarily acidic. In permanently acidic water, however, these species could not survive (Figure 2).

In particular for gammarids inhabiting flowing water, the flight reaction that leads to drifting with the current may be a life-saver in abrupt short-term decreases of pH levels, especially since the occasionally acidic parts of the water often extend only for a few hundred metres (BREHM 1980). After acidification has disappeared the survivors may move back into their previous habitat, or other individuals could newly migrate there. Again, Gammarus pulex is favoured here, which on account of its larger size and greater strength can move upstream more quickly than G. fossarum. This applies above all to male adult G. pulex, which therefore are sometimes found alone in certain parts of the water (MEIJERING 1971). This makes Gammarus pulex in at least three points more competitive with regard to water pH levels than its sister species G. fossarum: 1. It tolerates lower pH levels, 2. on account of its greater mobility it can more rapidly resettle brook regions that were temporarily acidified and thus depopulated, 3. it can more effectively regulate the pH level of the medium (interstitial systems of the bottom of water bodies) by means of its excretions.

The presence of heavy metals such as iron in the test water considerably raised the toxic effect of high hydrogen ion concentrations. In two extreme cases - their results have been omitted in Figures 5 and 6 for reasons of clarity - this causal relationship was proved or at least shown to be highly probable. Even the scatter of the measuring results that have been shown seems

to be partly due to an overlying toxic effect of heavy metals. The obviously lower toxicity of acidic spruce drip water might be explained by "masking" or complexing of heavy metals present, for the drip water contains large quantities of organic substances some of which bind and thus render heavy metals harmless even in more highly acidic medium. The acidic effect of the spruce drip water, i.e. the toxic effect of the hydrogen ions, is of course retained.

In this context it should also be mentioned that acidification in the field (for instance from sediments; cf. e.g. SCHINDLER et al. 1980) and in experiments in pond and brook water (from colloids) in principle always results in larger numbers of heavy metal ions being liberated. According to our own observations this applies especially in swamp springs temporarily acidified with sulphuric acid whose pH levels temporarily - in heavy precipitation after prolonged dry periods - may drop drastically. In the Schlitzerland, local pH levels dropped to almost 3 (BREHM 1980). The highly acidic water (sulphuric acid) contained large quantities of iron that had dissolved during bacterial pyrite oxidation (which also generates free sulphuric acid). In the field, very low pH levels therefore have highly toxic effects on the Daphnia and Gammarus species we investigated even indirectly via liberated heavy metal ions.

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Translation of German bibliographic entries:

1. Studies on the amino acid balance of Holstein bodies of water, in particular Lake Pluss.

2. On the anthropogenic acidification of the variegated sandstone forests of the Schlitzerland.

3. Comparative time studies on central European and Arctic representatives of the genus Daphnia (Phyllopoda, Crustacea). - Dissertation at the Department of Biology, Justus Liebig University, Giessen.

4. Occurrence of waterfleas (Cladocera) on the island of Spikeroog, 1960-1976.

5. The effect of marine storm tides on freshwater cladocerans.

6. The Gammarus fauna of the flowing waters of the Schlitzerland.

7. Experimental investigations on the drift and upstream migration of gammarids in flowing water.

8. Ecophysiological and production biological studies on juvenile stages of Gammarus fossarum KOCH 1835.

9. Ecological studies on Daphnia magna and Daphnia pulex in the field and in the laboratory.

10. The situation of the genus Gammarus in the Kaufunger Wald (Kaufung forest).

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